

Late Pleistocene glacial forest elements of Brazilian Amazonia

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ABSTRACT

Pollen data recovered from the sedimentary record of western Amazonia is still inadequate to fully address climate changes over the Last Glaciation in this region. The present work focuses vegetation dynamics from an area of southwestern Amazonia during the past 42,000 cal yr B.P. based on the integration of previous and new pollen data. Sediment cores were sampled from two sites covered by tropical rainforest in fluvial terraces of the Madeira River, a major southern Amazonian tributary. The results indicated a significant proportion of cold-adapted Andean tree species, represented by *Alnus* (0–20%), *Hedyosmum* (1–15%), *Podocarpus* (0–5%), *Illex* (1–11%) and *Weinmannia* (0–1%) at least between > 43,163–42,018 cal yr B.P. and 10,394–10,240 cal yr B.P. During the Holocene, only pollen representative of herbs and modern Amazonian vegetation persisted. The new pollen record confirmed previous documented results that vegetation communities presently restricted to Andean areas at altitudes higher than 2000–3000 m, occupied this region of the Amazonian lowlands close to the onset and probably also during the Last Glacial Maximum.

1. Introduction

Amazonian climate toward the onset and during the Last Glacial Maximum (LGM) has been a matter of intense debate. There is no consensus about the moisture variability, as both humid and arid conditions have been defended for the LGM in several Amazonian areas (Ab'Saber, 1977; Haffer, 1969; Haffer and Prance, 2001; Liu and Colinvaux, 1985; Tricart, 1985; van der Hammen and Absy, 1994; Vanzolini and Williams, 1981; Beerling and Mayle, 2006; Bush et al., 2004; Cheng et al., 2013; Colinvaux and De Oliveira, 2001; Colinvaux et al., 1996a; D'Apolito et al., 2013; Gosling et al., 2009; Van Der Hammen and Hooghiemstra, 2000; Irion, 1982; Maslin et al., 2011, 2012; Mayle and Beerling, 2004; Mayle et al., 2009; Mosblech et al., 2012; Räsänen et al., 1987; Rull, 2013). A recent work indicated that eastern Amazonia was drier during the last glacial period, with less water recycling and probably reduced plant transpiration, although the rainforest persisted over this time (Wang et al., 2017). Sedimentary record from Lake Pata in the western Amazonia lowlands suggests significantly drier climate during the middle Pleniglacial (60–35 ka - MIS3), late middle Pleniglacial (late MIS3) and LGM (MIS2). During this glacial period, herbs and taxa known to be dominant in seasonally dry forests were abundant, and cool-adapted elements were mixed with

warm lowland elements, which indicate a temperature depression (D'Apolito et al., 2013). Climate models have also suggested a progressive temperature decrease for the tropics during the LGM (Ganopolski et al., 1998; Gasse and Van Campo, 1998; Stute and Talma, 1998; Webb et al., 1997), but there are also disagreements regarding the temperature drop during this glacial event. According to CLIMAP (1976), temperature dropped by about 2 °C, while other studies indicated a decrease of as much as 4–6 °C (Cohen et al., 2014; D'Apolito et al., 2013; Van Der Hammen and Hooghiemstra, 2000) or even 12 °C below the modern mean temperature (Thompson et al., 1995).

Pollen records from Ecuador and Panama, together with the northward advance of *Araucaria* forests in southeastern Brazil (Bush et al., 1990, 1992; Ledru, 1993; Liu and Colinvaux, 1985; Pessenda et al., 2009; Piperno et al., 1990), provide evidence for significant cooling in glacial times. Measurements of sea surface temperature (SST) and noble gas concentration in fossil groundwater of eastern Brazil are consistent with cooling in the tropics during this period (Guilderson et al., 1994; Stute et al., 1995), as much as climate models support decreasing surface temperatures (Ganopolski et al., 1998; Gasse and Van Campo, 1998; Stute and Talma, 1998; Webb et al., 1997).

Pollen record from Lake Pata in the western Amazonian lowlands indicates glacial forest composition at the LGM (Colinvaux et al.,

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1996a). During this time interval, Amazonia was colonized by significant plant communities typical of modern montane areas. During the early Holocene global warming, plants intolerant to warmer climate retreated from the lowland forest (Colinvaux et al., 2000). Glacial-age pollen, phytolith and macrofossil data from lacustrine deposits at mid-elevations in Amazonian areas of Ecuador and Panama demonstrated significant plant populations currently restricted to elevations higher than 2000–3000 m growing at about 1000 m above modern sea level (Bush et al., 1990; Colinvaux et al., 1997; Liu and Colinvaux, 1985). Among these plant taxa were *Podocarpus*, *Drimys* and *Alnus*, none of which are present on the lower slopes of the Andes today. Therefore, pollen data suggest a response of Amazonian plant communities to temperatures colder than around 5–6 °C during glacial times (Bush et al., 2002; Colinvaux et al., 2000). Such evidence provides arguments for a lowland rainforest throughout the last glacial period with a distinctive composition than seen today in Amazonia (Bush, 2002). This, however, does not exclude the possibility of some peripheral areas currently with seasonal moisture deficits had been drier (Bush, 1994; Colinvaux et al., 1996a).

Previous pollen data from a core (HU-01) sampled in August 2010 near the Madeira River in the western Brazilian Amazonia indicated cold-adapted Andean plant elements, such as *Alnus*, *Hedyosmum*, *Weinmannia*, *Podocarpus*, *Ilex* and *Drymis* at least between > 42,600 and < 35,200 cal yr B.P. (Cohen et al., 2014). While pollen of herbs and tree taxa common to the modern Amazonian rainforest persisted through the Holocene, the cold pollen assemblage is restricted to the late Pleistocene. Pondering that Pleistocene data are based only on one core (HU-01), some doubts remained about the impact of the LGM on lowland (elevation of ~100 m) forests of western Amazonia and the meaning of this pollen signal in sedimentary deposits accumulated during the onset of the LGM. In order to better evaluate the LGM effects over this region, we present here the results of pollen analysis from two additional sediment cores sampled to the north and south of the previously documented core HU-01 (Fig. 1A). This work also includes descriptions of sedimentary facies and geomorphological data integrated with seven AMS radiocarbon and two optically stimulated luminescence (OSL) dating.

2. Study area

The study area is located near the town of Humaitá, south of the State of Amazonas in the western Brazilian Amazonia (Fig. 1A). This area presents surfaces with small elevation range (~100 m) and wide distribution of Quaternary deposits (> 500,000 km²) associated with savanna patches (Latrubesse and Franzinelli, 2002; Pessenda et al., 2001). It is characterized by tropical climate with a short dry season (Am in Köppen's classification), mean annual temperature between 25 °C and 26 °C, and mean low temperatures of about 20 °C in June and July. According to the Brazilian National Institute of Meteorology (INMET), the lowest temperature recorded in Porto Velho was 7.4 °C in July 1975, and the highest was 40.9 °C in August 1969. Precipitation averages 2250 mm/year, and the relative humidity is 85%. The rainy season begins in October, with precipitation peaks in January to February, while the dry season is between June and August (INMET - Instituto Nacional de Meteorologia, 2017).

2.1. Geological context and paleoenvironment

The study area is located in the foreland Solimões Basin. In addition to Paleozoic sequences, this basin includes the Alter do Chão (Cretaceous) and Solimões (Miocene) Formations, both inserted in the Javari Group (Cunha et al., 1994; Eiras et al., 1994). Plio-Pleistocene strata generically included in the Içá Formation (Caputo et al., 1972; Cunha et al., 1994), as well as Pleistocene-Holocene deposits (Rossetti et al., 2015) overly these units.

Deposits in the study area were formed in a fluvial system

influenced by tectonic reactivations during the late Quaternary (Hayakawa et al., 2010; Rossetti et al., 2008). The deposits occur mainly along river terraces and above the modern floodplain, with variations in altitude between 45 and 100 m (Bertani et al., 2015; Rossetti et al., 2015). Part of the fluvial deposition occurred within oxbow lakes. These lakes were formed by the deactivation of meanders during lateral channel migration. Such fluvial dynamics includes erosion of channel margins and further accretion in point bars. Oxbow lakes result from channel shutdown, and they are low-energy sites for the accumulation of fine-grained sediments from suspensions. A significant proportion of pollen grains preserved in oxbow lake deposits derives from the surrounding vegetation (Constantine and Dunne, 2008; Hager and Hutter, 1984; Keshavarzi and Habibi, 2005; Law and Reynolds, 1966).

2.2. Vegetation

The study area occurs in a region dominated by open vegetation in sharp contact with dense rainforest. Rainforest species are mainly represented by Euphorbiaceae, Bignoniaceae, Fabaceae, Moraceae, Anacardiaceae, Malpighiaceae, Malvaceae, Sapotaceae, Rubiaceae and Apocynaceae. Areas of open vegetation nearby the town of Humaitá, where the study area is located, cover approximately 615 km² (Vidotto et al., 2007). In these areas, Vidotto et al. (2007) identified 138 species and genera of woody and herbaceous vegetation, which are distributed among 37 families.

3. Material and methods

3.1. Remote sensing

The morphological mapping of the study area was based on a three-colour band composition (Red/Green/Blue = Band 5/4/3) of Landsat images acquired on September 2011. These optical images were downloaded from the Brazilian Institute of Space Research-INPE data bases and processed using the SPRING 4.3.3 software. The topographic data derived from the Shuttle Radar Topography Mission-SRTM, downloaded from the United States Geological Survey-USGS. Image interpretation of elevation data was carried out using the Global Mapper 12 software (Fig. 1B).

3.2. Field sampling and sediment description

This work was based on two sediment cores 7 m (PV37: 7° 29' 7.48"S/63° 0' 45.65"W) and 12 m (PV58: 8° 10' 31.31"S/63° 17' 43.07"W) in length (Fig. 1A and B). These were obtained using a Percussion Drilling System (Hammer Cobra TT), which allowed the recovery of continuous cores with 5.5 cm in diameter.

The cores were described in the field using characteristics such as lithology, texture and structure (Harper, 1984; Walker, 1992) annotated in measured lithostratigraphic profiles. Sediment grain sizes were determined by laser diffraction using a Laser Particle Size SHIMADZU SALD 2101 in the Laboratory of Chemical Oceanography of the Federal University of Pará (UFPA). Details about laboratory procedures for sediment size analysis were presented in França et al. (2013).

3.3. Palynological analysis

In order to determine the pollen content, a total of 180 samples measuring 1.0 cm³ were taken at 5.0 (PV-58) and 10 cm (PV-37) intervals. The samples were processed according to standard pollen analytical techniques (Faegri and Iversen, 1989). The identification of pollen and spores was based on reference collections (Absy, 1975; Colinvaux et al., 1999; Markgraf and D'Antoni, 1978; Roubik and Moreno, 1991; Salgado-Labouriau, 1973). The pollen data base of the Laboratory of Coastal Dynamics from the UFPA and ¹⁴C Laboratory of

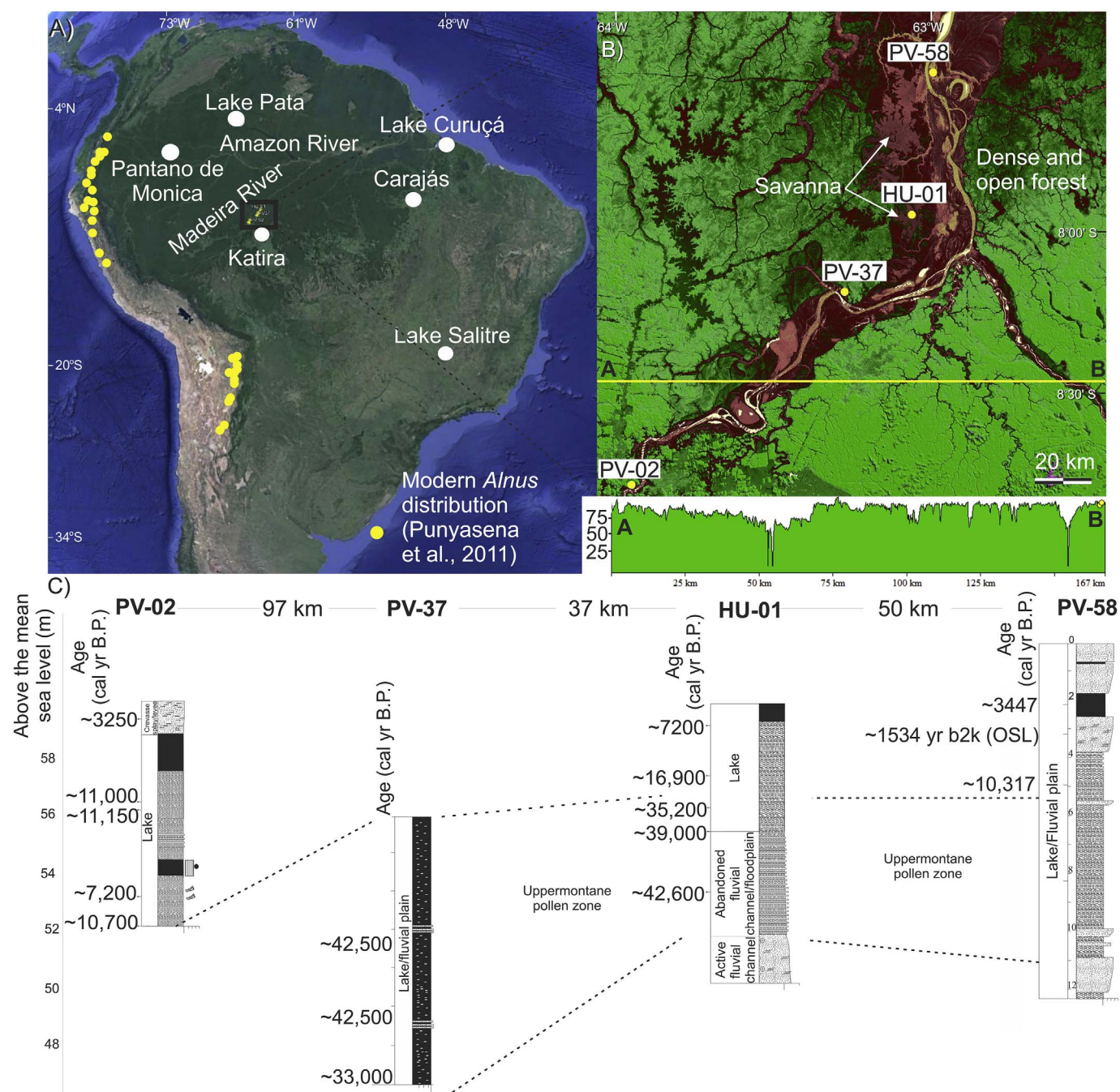


Fig. 1. Location of the study area: A) Modern *Alnus* distribution (Punyasena et al., 2011), study site of previous studies about the LGM in Brazil (Absy et al., 1991; Behling, 2001; Colinvaux et al., 1996a; Ledru, 1993; van der Hammen and Absy, 1994; Van der Hammen, 2000); B) main geomorphologic features based on SRTM data, sampling sites of the studied cores and topographic profile; C) Pleistocene glacial pollen zone based on correlation between the cores PV-02, HU-01 (Cohen et al., 2014), PV-37 and PV-58.

the Center for Nuclear Energy in Agriculture (CENA/USP) also supported the identifications of pollen taxa. The low pollen concentration usually required a minimum counting of 150 pollen grains per each sample. Forty-two pollen taxa were recognised (Table 1) and distributed in ecological groups. The pollen diagrams were statistically subdivided into pollen assemblage zones based on cluster analysis (Grimm, 1987). Some intervals with absence or only a few pollen grains (< 3000 grains/cm³) were related to factors such as sediment grain size, microbial attack, oxidation and/or mechanical forces. They can also be due to characteristics inherent to pollen grains, such as sporopollenine content, as well as the chemical and physical composition of pollen walls (Havanga, 1967). In addition, pollen grains tend to decay rapidly in sandy sediments when compared to muddy deposits. This is

due to the better drainage of sands caused by large interstitial pores, which allows pollen grains abrade by mobile inorganic matrix and oxidized during soil hydration-dehydration cycles (Faegri, 1971; Grindrod, 1988).

3.4. Radiocarbon and OSL dating

The chronology of sedimentary deposits from cores PV-48 and PV-37 was based on radiocarbon analysis of sedimentary organic matter from seven samples (10 g each) (Table 2). Radiocarbon analyses were undertaken at the BETA Analytic Laboratory using an accelerator mass spectrometer (AMS). The measured ages were normalized to a $\delta^{13}\text{C}$ of -25‰ VPDB and reported as calibrated years (cal yr B.P.) (2σ) using

Table 1
Pollen taxa identified in the PV-37 and PV-58.

Taxa	Taxa	Taxa
Acanthaceae	Betulaceae	Malvaceae
Aizoaceae	Bignoniaceae	Marantaceae
<i>Alnus</i>	<i>Borreria</i>	<i>Mauritia</i>
<i>Alternanthera</i>	Burseraceae	Melastomataceae/Combretaceae
Amaranthaceae	Chloranthaceae	Meliaceae
Anacardiaceae	Cunoniaceae	<i>Mimosa</i>
<i>Anacardium</i>	Cyperaceae	Moraceae/Urticaceae
Annonaceae	<i>Didymopanax</i>	Myrtaceae
<i>Annona</i>	Ericaceae	Poaceae
Apocynaceae	Euphorbiaceae	<i>Podocarpus</i>
Aquifoliaceae	Fabaceae	<i>Protium</i>
Araliaceae	<i>Hedyosmum</i>	Rubiaceae
Arecaceae	<i>Ilex</i>	Sapotaceae
Asteraceae	Malpighiaceae	<i>Weinmannia</i>

Table 2
Sediment samples selected for radiocarbon dating and results with code site, laboratory number, depth, material, ^{14}C yr B.P. and calibrated (cal) ages.

Lab. number (beta)	Core	Depth (M)	Age (^{14}C yr B.P.)	Age (cal yr B.P., 2 σ)	Mean age (cal yr B.P., 2 σ)
304,803	PV-37	3.4–3.5	38,400 $\pm$ 330	42,911–41,991	42,450
09810	PV-37	5.2–5.3	38,620 $\pm$ 420	43,163–42,018	42,590
304,801	PV-37	6.7–6.8	29,040 $\pm$ 160	33,643–32,762	33,200
406,692	PV-58	2.2–2.3	3300 $\pm$ 30	3509–3385	3447
397,689	PV-58	4.9–5	9210 $\pm$ 30	10,394–10,240	10,317
406,694	PV-58	8.2–8.3	6110 $\pm$ 40	7000–6790	6900
397,690	PV-58	9.55	3410 $\pm$ 30	3635–3475	3555

the CALIB 6.0 software and SHcal13 curve (Reimer, 2013). Two samples were analyzed by OSL at the Luminescence and Gamma Spectrometry Laboratory (LEGaL) from the University of São Paulo (USP-SP). OSL is used to estimate the time elapsed since buried sediment grains were last exposed to daylight. This method of sediment dating considers that the daylight releases charge from light-sensitive traps of crystals such as quartz and feldspar, which resets the OSL signal. When the grains are buried, they begin to accumulate a trapped charge population owing to ionising radiation (Murray and Olley, 2002). A sample in which the mineral grains have been exposed to sufficient daylight can be said to be of zero age (Preusser et al., 2008). The lower age limit in luminescence dating is determined by the OSL sensitivity and detection limit of this signal in relation to the background. Then, OSL ages can be determined typically from a few decades (e.g. Sawakuchi et al., 2008) up to 350,000 years (Murray and Olley, 2002). The OSL ages are reported as b2k years (before the year 2000) (Table 3). Details about the laboratory procedures may be obtained from Rossetti et al. (2015).

4. Results and discussions

4.1. Dating

Radiocarbon and OSL ages are ranged from 43,163–42,018 cal yr B.P. (^{14}C AMS) to 1534 $\pm$ 270 yr b2k (OSL) (Tables 2 and 3). The old records for both cores contain age inversions (Figs. 2 and 4), which are

Table 3
OSL dated samples with corresponding depths, recycling rates, total annual dose rate (AD), equivalent doses (De), and OSL ages.

Lab. number (LEGaL)	Core	Depth (M)	Recycling rate	Dose rate (Gy/ka)	DE (Gy)	OSL age (CAM)	OSL age (B2K)
L0281	PV-58	3.2–3.3	0.99 $\pm$ 0.06	2.39 $\pm$ 0.20	3.7 $\pm$ 0.58	1549 $\pm$ 275	1534 $\pm$ 275
L0282	PV-58	11.4	0.98 $\pm$ 0.04	1.52 $\pm$ 0.13	3.2 $\pm$ 0.43	2106 $\pm$ 332	2091 $\pm$ 332

CAM – Central Age Model. B2k – before the year 2000.

attributed to low sediment deposition, younger carbon contamination and/or reworking of older sedimentary organic matter, as well as differences in the dating methods (see section PV-58 – Late Pleistocene).

4.2. Morphological context and sedimentological analysis

The sampling sites present dense and open forest, but some natural savanna patches occur distributed in the study area. The cores PV 58 and PV 37 were taken from old fluvial terraces located respectively $\sim$ 15 m and 7 m higher than the Madeira River modern floodplain (Fig. 1A). They derive from a meander paleolandform preserved on the surface of a fluvial terrace. Sedimentological analysis revealed massive and laminated mud, massive and cross-stratified sand, and heterolithic bedded deposits (Table 4 and Figs. 2 and 4). At the base of core PV-58, between 12.3 and 10 m depth, the sediments varied in grain size (sand = 70–10%, silt = 70–20% and clay = 30–10%). The predominance of muddy sediments occurred in the interval between 10 and 4 m (sand = 10–40%, silt = $\sim$ 50%, clay = 40–10%). Sands (sand = 70%, silt = 15%, clay = 15%) were alternated with muds (sand = $\sim$ 20%, silt = $\sim$ 45%, clay = $\sim$ 25%) in the uppermost 4 m of the core. The core PV-37 was dominated by muddy sediments (sand: $\sim$ 20%, silt: $\sim$ 60%, clay: $\sim$ 20%) throughout its 7 m of depth.

These foregoing descriptions are consistent with muddy deposition from suspensions in abandoned channels and/or floodplains. We interpret that the pollen bearing sediments record stagnant conditions within mud plugs or small lakes developed on floodplains (Figs. 2 and 4).

The abandoned channels are dominantly covered by herbaceous vegetation (Fig. 1b). A recent publication from this area stated that the establishment of savanna during the Holocene was related to the progressive deactivation of river channels and oxbow lakes (Rossetti et al., 2017). Such process culminated with sediment filling and subsequent subaerial exposure, which provided new sites for plant colonization, first by herbs and then dense forests (Amaral et al., 2012).

4.3. Core PV-37 (Late Pleistocene)

The radiocarbon ages from core PV 37 revealed late Pleistocene ages (42000–33,000 cal yr B.P.) in wavy and lenticular bedded deposits. The pollen record showed the significant occurrence of taxa adapted to cold climate (0–22%), such as *Alnus* (20%), *Hedyosmum* (10%) and *Podocarpus* (5%). Herb pollen (10–100%) consisted of Poaceae (10–100%), Cyperaceae (0–50%) and Asteraceae (0–18%). Modern representative taxa from the Amazonian forest (10–90%) were mainly of Euphorbiaceae (5–45%), Moraceae/Urticaceae (5–25%), Fabaceae (5–25%), Rubiaceae (0–24%), Myrtaceae (0–70%), Apocynaceae (0–10%), Malpighiaceae (0–5%) and Acanthaceae (0–10%). Palm pollen (0–20%) were also present (Figs. 2 and 3).

4.4. Core PV-58 (Late Pleistocene)

Pleistocene ages were not recorded along this core, but considering the Holocene ages obtained between 0 and 5 m, the interval between 5 and 12.2 m was probably deposited during the late Pleistocene (Fig. 4). Thus, the ages of 7000–6790 cal yr B.P. and 3635–3475 cal yr B.P. obtained from 8.25 m and 9.55 m depth, respectively, were likely too young. Younger carbon contamination at these depth may have

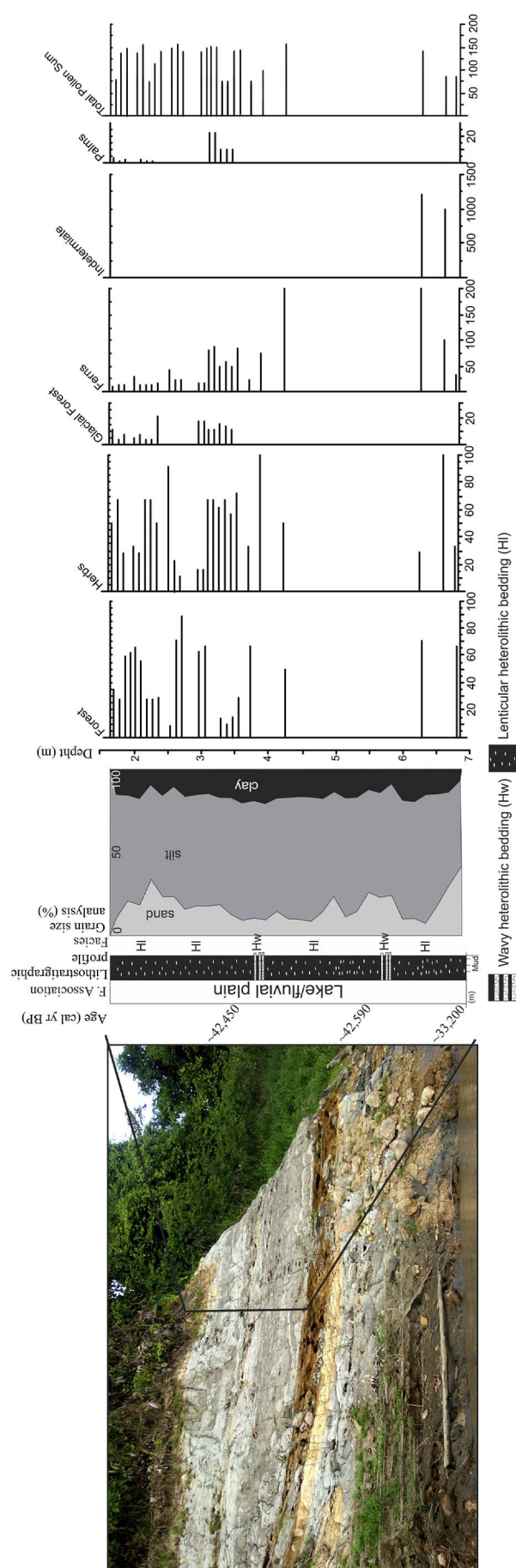


Fig. 2. Summarized results for core PV-37, with variation as a function of core depth showing chronological and lithological profiles with sedimentary facies, as well as ecological pollen groups. Pollen data are presented in the pollen diagrams as percentages of the total pollen sum.

occurred by root activity, infiltration of dissolved organic components, influence of microorganisms, and of soil fauna (Pessenda et al., 2001). Although the humin often contains the most resistant and immobile organic molecules (Pessenda et al., 2001; Stevenson, 1994), rejuvenation of organic components might occur owing to the inclusion of organic molecules from young roots (Orlova and Panychev, 1993; Nierop et al., 1999). Our samples were examined and physically cleaned under a stereomicroscope to avoid possible contamination by shell fragments, roots and seeds. In addition, a rigorous pretreatment for the extraction of the humin from sediment samples with acid–alkali–acid method was used for our samples (Pessenda et al., 1996). However, some contamination by residual fractions of roots may occur (Pessenda, personal communication). The longer exposure to contamination by roots, the greater the rejuvenation. Additionally, the rejuvenating impact of fresh roots is higher on samples with low ^{14}C activity than on samples with high ^{14}C activity (Mook and van de Plassche, 1986).

Similarly to the foregoing discussed rejuvenation problem of radiocarbon ages, the OSL age of 2091 ± 330 yr b2k for a sample located at 11.4 m depth is also likely too young. The combination of radiocarbon and OSL dating has provided a complementary chronology for lake sediments (Mischke et al., 2017). However, fluvial dynamics may have affected the OSL signal in the study area. One possibility is that the sediment from 11.4 m depth was deposited within a channel deeply incised into older, but erosive surfaces or sandy sediments were not identified at this stratigraphic interval of core PV-58. A more plausible explanation for this young OSL age is chemical weathering. Sediments can be submitted to changes in water content, elemental concentration, and mechanical properties in the course of chemical weathering. These processes likely result in changes of dose rate and equivalent dose by redistribution of radioactive elements, which produce inconsistency (overestimation or underestimation) in OSL ages (Jeong et al., 2007).

Therefore, the most likely to consider is that the ages obtained above 5 m depth are the most reliable, which means that the deposits below this depth are most likely within the range of Pleistocene. The LGM is commonly lost in lowland tropical South America, where a hiatus in sedimentation have been commonly recorded. For instance, a hiatus in sedimentation was recorded between 23,000 and 13,000 ^{14}C yr B.P. in Carajás (Absy et al., 1991), 30,000 and 16,000 ^{14}C yr B.P. in Maicuru (Colinvaux and De Oliveira, 2001), and 38,600 and 11,030 ^{14}C yr B.P. in Laguna Bella Vista (Sifeddine et al., 2001). An analogous situation was identified by Cohen et al. (2014) in the core HU-01, where a hiatus in lacustrine sedimentation occurred between 35,584–34,804 cal yr B.P. and 17,065–16,717 cal yr B.P. (Fig. 1C). However, a sedimentological and geomorphological study of the Solimões-Amazon River alluvial plain recorded the LGM in central Amazonian lowlands by formation of fluvial terraces between 25,300 cal yr B.P. and 17,700 cal yr B.P. (Sant'Anna et al., 2017).

In the particular instance of the study area, an erosive event was not identified below 5 m depth. On the contrary, the deposits below this depth consist of an interval of mostly mud lacking any evidence of weathering, pedogenesis or erosional contacts. However, the prevalence of muddy deposits is consistent with a sedimentation rate lower than above 5 m depth, where sandy deposits dominate. Assuming a low sedimentation rates, the most likely is that the interval below 5.5 m includes LGM and older Pleistocene deposits.

It is interesting to note that, similarly to the late Pleistocene deposits of core PV-37 (Fig. 2), the pollen record below 5 m depth indicated an assemblage representative of taxa currently found under climates colder than the present one, which is represented by *Illex* (1–11%), *Hedyosmum* (1–15%), *Alnus* (0–4%), *Weinmannia* (0–1%) and *Podocarpus* (0–1%) (Figs. 4 and 5). Therefore, we assume that at least part of the sediments below 5 m depth in core PV58 was accumulated during the late Pleistocene.

The herb pollen were represented by Poaceae (15–100%), Asteraceae (2–30%), *Alternanthera* (0–9%), Amaranthaceae (0–15%),

Table 4

Lithofacies descriptions of cores PV-37 and PV-58.

Facies	Abbreviations	Sedimentary process
Massive sand	Sm	Deposition episodic from sand inflow into the environment (Crevasse splay)
Massive mud	Mm	Sediment homogenization biological activity and/or pedogenic processes.
Wavy heterolithic deposits	Hw	Alternation in power flow, with a balance between depositions of clay from suspension of sand.
Lenticular heterolithic deposits	HL	Low flow energy suspension, but with periodic sand inflows.
Parallel laminated mud	Mlp	The mud deposition occurs by suspension under low energy flow. Heterolithic deposits also represented low energy, but with episodic input sand higher energy flow.
Cross laminated sand	Scl	Deposition from the migration shaped in the lower bed flow. Constant oscillation flow with deposition from the traction, alternating with episodes of deposition suspensions.

Cyperaceae (0–1%), *Borreria* (0–5%) and Aizoaceae (0–1%). The modern representative taxa from Amazonian forest (5–50%) consisted mainly of Moraceae/Urticaceae (5–25%), Malpighiaceae (0–15%), Euphorbiaceae (0–35%), Fabaceae (5–30%), *Mimosa* (5–30%) Rubiaceae (0–20%), Apocynaceae (0–20%), Melastomataceae/Combretaceae (0–5%), Myrtaceae (0–5%), *Anacardium* (0–10%) and *Protium* (0–10%). Palm pollen (3–45%) were also present (Fig. 5).

4.5. Core PV-58 (Holocene)

Herbaceous pollen (40–100%), mostly Poaceae (20–100%), Asteraceae (0–50%), *Alternanthera* (0–35%) and Amaranthaceae (0–18%) dominated the last 10,394–10,240 cal yr B.P. This period recorded high values of taxa currently found in the Amazonian forest, mainly represented by Moraceae/Urticaceae (0–15%), Malpighiaceae (0–70%), Euphorbiaceae (0–50%), Fabaceae (0–50%), *Mimosa* (0–5%) Rubiaceae (0–15%), Apocynaceae (0–2%), Melastomataceae/Combretaceae (0–15%) and *Anacardium* (0–5%). Palm pollen (0–80%) are also present. Taxa currently found under colder climates were absence in the Holocene deposits of this core (Figs. 4 and 5).

5. Impacts of late Pleistocene glacial periods on South America

The Last Glacial Maximum (LGM) is generally associated with global ice sheet expansion at ~ 26,500–19,000 years ago, mainly in the northern hemisphere (Clark et al., 2009). Although some models indicate that the Antarctic Ice Sheet experienced significant expansion and retreat during and after the LGM, respectively (Denton and Hughes, 2002; Huybrechts, 2002; Nakada et al., 2000; Pollard and DeConto, 2009), the Antarctic Ice Sheet dynamics during and after the LGM remains controversial (Anderson et al., 2002; Weber et al., 2011). However, some studies suggest that the LGM may have impacted the Amazonia region (e.g. Anhuf et al., 2006), with cold air being brought as far north as the Equator. An increased invasion of cold air, as considered by the Mobile Polar High concept of Leroux (1993), could explain the vegetation changes recorded in the study area. The magnitude of these changes in western Amazonia during the time preceding the LGM, which corresponds to the Marine Isotope Stage 3 (MIS3, between 60 and 27 ka), are unknown owing to the lack of palaeoecological data. Temperatures were 2 °C warmer than in the LGM worldwide (Van Meerbeek et al., 2009).

Reconstructions have been performed to examine the impacts of the last glacial period at regional scale over the Amazonian region. For instance, the maximum glacial occurred before 24,000 cal yr B.P. in the central Andes and terminal moraines were dated at their lowest elevation in Bolivia at ~ 34,000 cal yr B.P. (Klein et al., 1999; Smith et al., 2005). The LGM in the Titicaca region, defined as 26,000–22,000 cal yr B.P. (Weng et al., 2006), was wetter and about 5°–8 °C colder than today (Abbott et al., 2000; Baker et al., 2001; Paduano et al., 2003). Palaeoecological studies in southeastern Peru (1360 m above sea-level, asl) and in northeastern Bolivia (600 to 900 m asl) near southern Amazonia revealed forests dominated by lowland elements and upper montane taxa, such as *Podocarpus*, *Alnus* and *Ilex* between 43,500 and

22,000 cal yr B.P. and between 50,000 cal yr B.P. and the late glaciation, respectively (Burbridge et al., 2004; Urrego et al., 2005).

The onset of deglaciation of the West Antarctic Ice Sheet occurred between 15,000 and 14,000 cal yr B.P. (Clark et al., 2009), while in the Andes it began between 21,000 and 19,000 cal yr B.P. (Clark et al., 2002). Near the upper forest limit of the eastern Peruvian Andes, pollen, charcoal, and sedimentary data suggest that the deglacial period occurred from ca. 17,000 to ca. 11,500 cal yr B.P. (Bush et al., 2005), while at Lake Titicaca pronounced warming between 13,000 and 12,000 cal yr B.P. established near-modern temperatures (Paduano et al., 2003; Ybert, 1992).

6. Pleistocene glacial forest of Brazilian Amazonia

The impact of Pleistocene glaciations on the Amazonian rainforest has been intensely debated. The discussion has concentrated mainly on whether: 1) the Amazonian rainforest was fragmented in refuge islands or its area remained relatively stable; 2) the floristic composition changed by connections with the Andean and Atlantic rainforest ecosystems (Colinvaux et al., 1996a; Colinvaux and De Oliveira, 2001; Haffer and Prance, 2001; Van Der Hammen and Hooghiemstra, 2000).

This work and a recent publication (Cohen et al., 2014) contribute to the discussions about whether the floristic composition of Western Amazonia was submitted to species re-associations with Andean vegetation according to late Pleistocene temperature reduction. One core from Humaitá (core HU-01, Fig. 1C), south of the State of Amazonas, indicated pollen community of herbaceous vegetation, some modern representative taxa from Amazonian forest and cold-adapted plants from Andes, which were represented mainly by *Alnus* (2–11%), *Hedyosmum* (2–17%), *Weinmannia* (0–18%), *Podocarpus* (0–4%), *Ilex* (0–4%) and *Drymis* (0–1%) at least between > 42,030–43,170 cal yr B.P. and < 34,800–35,580 cal yr B.P. The herbaceous vegetation persisted during the Holocene, whilst the cold pollen assemblage became extinct in the western Amazonian lowlands (Cohen et al., 2014). The fact that the present study also indicates an expressive percentage of some taxa adapted to cold forest during the late Pleistocene, such as *Alnus* (0–20%), *Hedyosmum* (1–15%), *Podocarpus* (0–5%), *Illex* (1–11%) and *Weinmannia* (0–1%) suggests a wide glacial impact over this region following a transect of ~ 190 km (SW-NE) along the paleo-floodplain of the Madeira River (Fig. 1B).

In general, western Amazonian lowlands have provided few pollen data, with the results presented in this work being the only successful record produced by the analysis of twenty other sediment cores sampled from this region. As described in the palynological analysis section, this low pollen preservation may have been caused by various external factors, such as sediment grain size, microbial attack, oxidation and mechanical forces (Havinga, 1967). Mainly along the core HU-01, the low pollen preservation along mud sediments is probably due to an oxidizing environment that is recorded by mud with iron staining and ferruginous nodules that may be related to a dry period during the late Pleistocene (Cordeiro et al., 2011) and in the early and mid-Holocene (Mayle et al., 2000; Mourguiart et al., 1998; Pessenda et al., 2001) in distinct locations of the Amazon and Andes region. According to

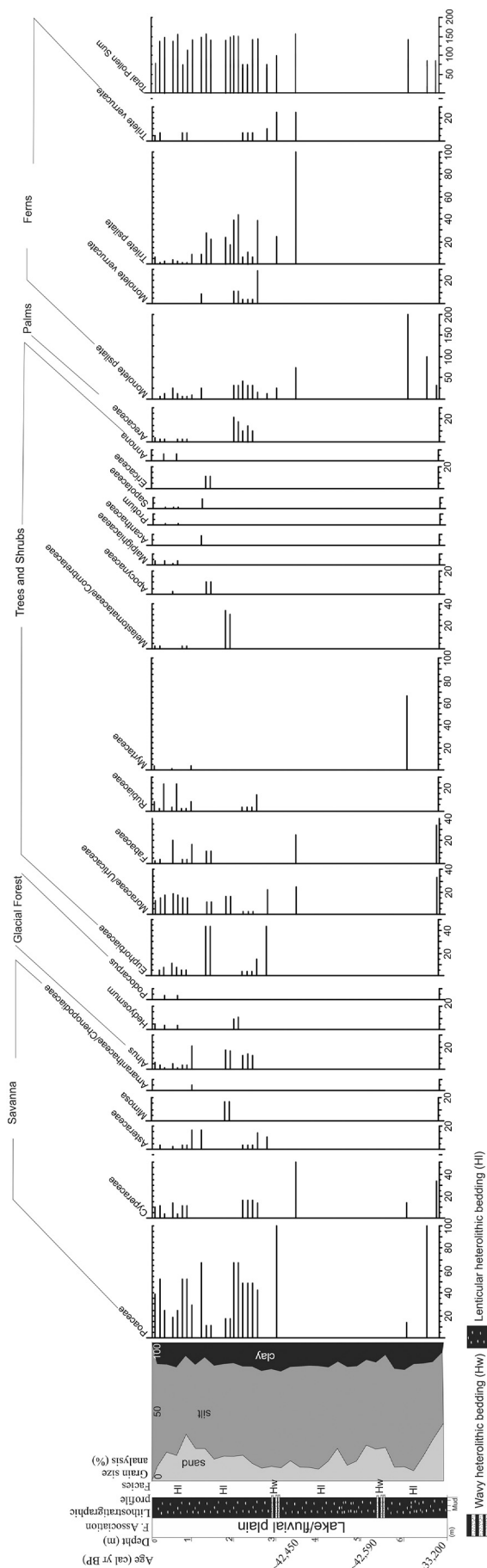


Fig. 3. Pollen diagram record for core PV-37, with percentages of the most frequent pollen taxa and samples age.

Argollo and Mourguiart (2000) two long arid phases occurred during the LGM and in the early and middle Holocene in the Andes.

Pollen data from Lake Pata in the Hill of Six Lakes, in NW Amazonia, demonstrated that the tropical rainforest occupied the region continuously and that savannas or grasslands were not present during the LGM. These data suggest that the western Amazonian forest was not fragmented into refugia in glacial times. Glacial age forests were comparable to modern forests, but also included species now restricted to higher elevations by temperature, suggesting a cooling of the order of 5° to 6 °C (Colinvaux et al., 1996b).

According to Bush et al. (2004), pollen and paleochemical data indicated that the Hill of Six Lakes presented oscillations of lake level during the last 170,000 years, where the lowstands are attributed to reduced precipitation inputs to systems. The strongest of eight lowstand cycles occurred ca. 35,000 to 27,000 cal yr B.P. Biogeochemical data of another sediment core from Lagoa da Pata in the Hill of Six Lakes indicated two phases of relatively high lake level, from ca. 50,000 cal yr B.P. until 26,300 cal yr B.P. and from 15,300 cal yr B.P. until 10,000 cal yr B.P. (Cordeiro et al., 2011). According to these authors, these phases were separated by a period of lowered lake level from 26,300 cal yr B.P. until 15,300 cal yr B.P., suggesting a dry period. New analyses of a sedimentary record of Lake Pata indicated that the hill remained forested; however, there were clear signals of structural change, which indicate that the area experienced a significantly drier climate during the middle Pleniglacial (60,000–35,000 cal yr B.P. - MIS3), late middle Pleniglacial (late MIS3) and LGM (MIS2). Herbs and taxa known to be dominant in seasonally dry forests were all more abundant during the glacial part of the record, and the cool-adapted elements were mixed with warm lowland elements, which indicate a temperature depression. (D'Apolito et al., 2013).

Whether the Amazon basin was drier or wet during glacial times remains open for debate, as most study sites are located on the periphery of the basin and the interpretations can be complicated by sediment preservation, uncertainties in chronology and topographical setting. Wang et al. (2017) show that rainfall in the basin responds closely to changes in glacial boundary conditions in terms of temperature and atmospheric concentrations of carbon dioxide. The oxygen isotopic record of the past 45,000 years of speleothems from Paraíso Cave in eastern Amazonia indicated that, relative to modern levels, precipitation in the region was about 58% during the Last Glacial Maximum (around 21,000 years ago) and 142% during the mid-Holocene epoch (about 6000 years ago).

Additional studies based on modern arboreal/herbs pollen rates to compare with LGM and Holocene pollen signals along the studied cores could be proposed to contribute to discussions about aridity during these periods. However, a recent work (Rossetti et al., 2017) in the study area suggests that savanna patches developed over terraces of the Madeira River since the mid-Holocene and their maintenance up to the present have responded mainly to sedimentary dynamics, rather than to climate changes. Therefore, modern and stratigraphic records of the arboreal/herbs rate could have a significant contribution of herbaceous pollen grains sourced from savannas formed by sedimentary processes. It would prevent an adequate analysis of the humidity changes in the study area during the late Pleistocene.

Regarding temperature, the integration of our data confirms the presence of glacial forest in the Western Amazon region during the late Pleistocene, mainly due to the presence of *Alnus* pollen in the lower part of the studied cores. This is because modern biogeographic data indicate that *Alnus* covers whole mountain sides, at about 2000–3000 m, where mean annual temperatures are between 8 and 18 °C and minimum winter temperatures are no lower than −10 °C along the Andes and Central America (Fig. 1A) (Furlow and Furlow, 1979; Punyasena et al., 2011; Weng et al., 2004b). In Central America, areas of maximum representation of *Alnus* in the pollen rain varies from 20% to 60% (Bush, 2000). In southern Peru, *Alnus* pollen values of < 2% are almost certainly attributed to long distance dispersal, while its presence

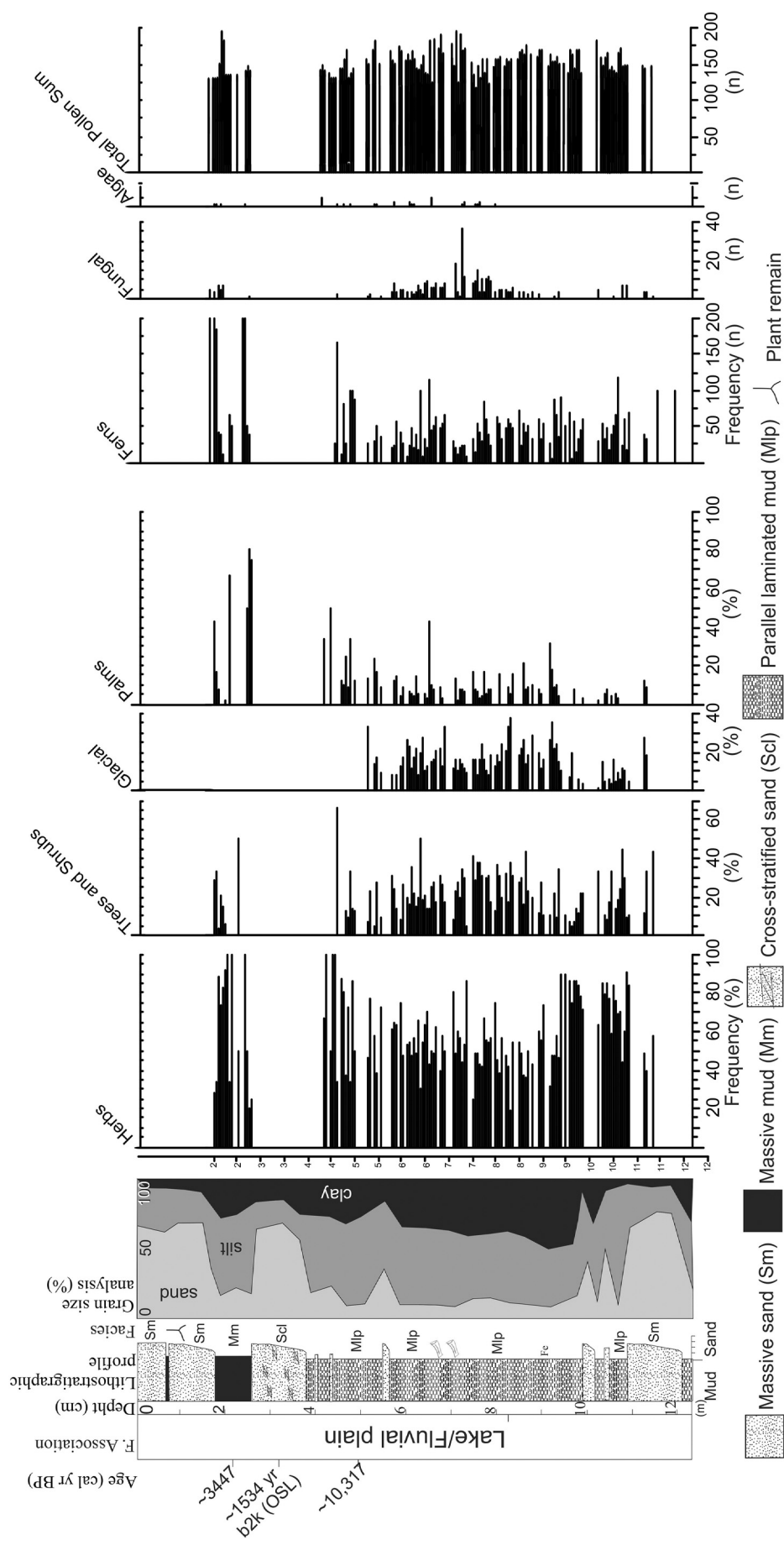


Fig. 4. Summarizing results for core PV-58, with variation as a function of core depth showing chronological and lithological profiles with sedimentary facies and ecological pollen groups. Pollen data are presented in pollen diagrams as percentages of the total pollen sum.

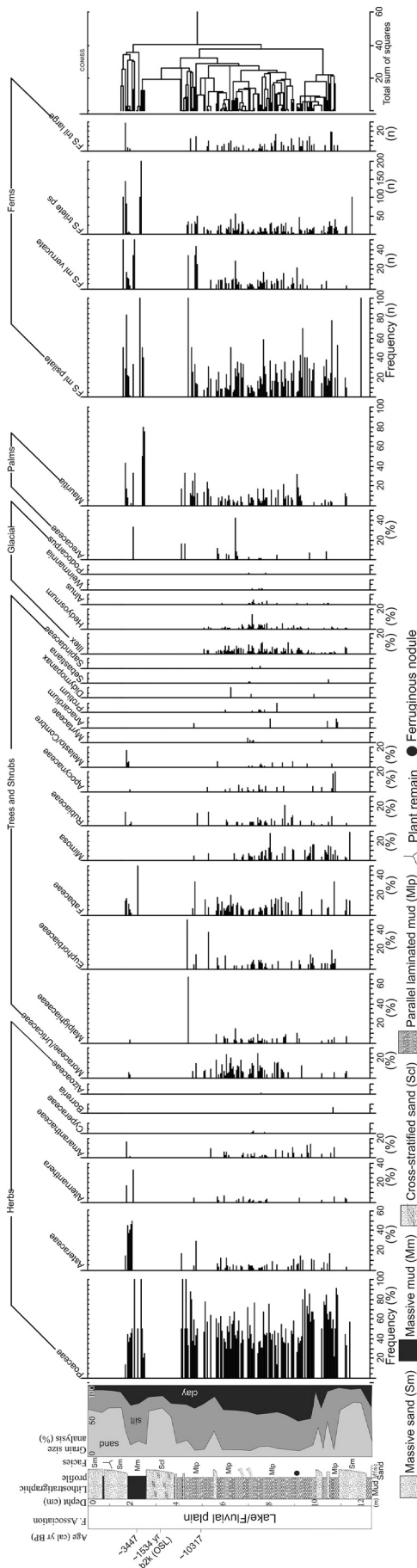


Fig. 5. Pollen diagram record for core PV-58, with percentages of the most frequent pollen taxa, samples age, zones and cluster analysis.

at > 5% probably indicates the local occurrence of this plant (Weng et al., 2004a, 2004b). *Alnus* pollen are present between 4 and 13% in samples collected above 2300 m, indicating the presence of *Alnus* trees in the moist Andean forest (Reese and Liu, 2005; Weng et al., 2004a).

Regarding the Pleistocene *Alnus* pollen, the Andean flank in western Amazonia presented percentage with values between 2% and 40% (Cárdenas et al., 2011). *Alnus* pollen were also recorded in several studies focusing the Quaternary of Brazil (Absy, 1979; Behling et al., 2004; Colinvaux et al., 1996a, 1996b). However, *Alnus* occurs in low percentage values in these records, since it is not native in Brazil and has a wind dispersal for hundred kilometers from *Alnus* trees (Davis et al., 1973; Davis and Deevey, 1964). In these studies, this taxon occurred with < 1% in lake sediments and in soil surface (Absy, 1979; Behling et al., 2004; P.A. Colinvaux et al., 1996b). Sediments from the Amazon River and Southern Brazil recorded pollen *Alnus* with < 5% and < 2% during the LMG, respectively (Haberle, 1997; Macedo, 2009).

The abundance of highland taxa in the lower portions of the cores PV-37, PV-58 and HU-01 and the absence of montane elements from the top of the cores PV-58, PV-02 and HU-01 are related to the late Pleistocene glacial period and Holocene warmer climate (Fig. 1C). Considering the integration of the studied cores, the uppermontane taxa assemblage, represented by *Weinmannia*, *Hedyosmum*, *Podocarpus* and *Ilex*, is characterized by pollen types less spread and/or yielded in low quantities relative to *Alnus* pollen (Weng et al., 2004b). This is an evidence that cold-adapted plants migrated to terraces near lakes and zones topographically higher than fluvial plains in the study area during the late Pleistocene, while the *Alnus* trees could have expanded to zones relatively more distant from the study area.

The possibility of wind and fluvial pollen transportation from Andean areas is ruled out, as cold forest pollen were not recorded in the Holocene succession, which would be predicted in the case of wind transportation from Andean areas. Additionally, based on facies analysis, sediments were deposited in a low energy depositional environment disconnected from the main stream, which minimizes the possibility of pollen sourced from Andean areas by fluvial transportation. A broad discussion about the possibility of wind and fluvial pollen transportation from Andean areas may be found in Cohen et al. (2014).

Therefore, based on previous palaeoecological studies, the lowland Amazonian rainforest was submitted to a cooling (5–9 °C) during the LGM (Bush et al., 2004), and there was a mixture of both lowland elements and uppermontane in the western Amazonian lowlands in the onset of the LGM (Cohen et al., 2014). The present study allows expand geographically the interpretations about the lowland Amazon vegetation during the late Pleistocene and corroborates the presence of areas occupied by taxa adapted to cold climate (*Ilex*, *Hedyosmum*, *Podocarpus* and *Alnus*) in Western Amazonia. In addition, it complements studies on the impact of the LMG on the Amazonian lowlands and others regions of Brazil (Table 5) (Absy et al., 1991; Behling, 2001; Cohen et al., 2014; Colinvaux et al., 1996a; Ledru, 1993; Ledru et al., 2001; Sifeddine et al., 1994; van der Hammen and Absy, 1994; Van der Hammen, 2000). The present findings are in good agreement with Rind's models, in which changes in latitudinal temperature gradient affect large-scale atmospheric dynamics (Rind, 2000).

7. Conclusions

Pollen analysis combined with sedimentological descriptions of four sediment cores positioned in a transect of ~ 190 km (SW-NE) along the paleo-floodplain of the Madeira River indicated the existence during the late Pleistocene of modern Amazonian taxa and Andean cold-adapted plants represented by *Alnus* (0–20%), *Hedyosmum* (1–15%), *Podocarpus* (0–5%), *Ilex* (1–11%) and *Weinmannia* (0–1%). The abundance of highland taxa between > 43,163–42,018 cal yr B.P. and 10,394–10,240 cal yr B.P. and the absence of glacial forest elements during the Holocene stratigraphic succession indicate a distinction

Table 5
Sites providing dated information of LGM ecological conditions based on pollen in Brazil.

Glacial pollen	Location	Distance	Radiocarbon age (cal yr B.P.)	Reference
<i>Illex</i> (0–5%); <i>Podocarpus</i> (0–1%) and <i>Weinmannia</i> (0–2%).	Katira 9°S/63°W	≈ 97 km	≈ 40,000	Van der Hammen and Absy (1994)
<i>Podocarpus</i> (0–50%); <i>Illex</i> (0–35%); <i>Weinmannia</i> (0–35%); <i>Humiria</i> (0–35%); <i>Hedyosmum</i> (0–30%) and <i>Rapanea</i> (0–25%).	Lake Pata 0°16'N/66°41'W	≈ 1000 km	> 40,000	Colinvaux et al. (1996b)
<i>Illex</i> (0–8%); <i>Drymis</i> (0–1%) and <i>Podocarpus</i> (0–1%).	Lake Salitre	≈ 2100 km	28,000	Ledru (1993)
<i>Illex</i> (0–40%); <i>Podocarpus</i> (0–3%)	Carajás 6°20'S/50°25'W;	≈ 1400 km	26,000–15,000	(Absy et al., 1991; Sifeddine et al., 1994; Ledru et al., 2001)
<i>Illex</i> (0–15%); <i>Podocarpus</i> (0–1,5%)	Pantano de Monica 0°42'S/72°04'W	≈ 1300 km	17,000–13,000	Van der Hammen (2000)
<i>Hedyosmum</i> (0–20%); <i>Weinmannia</i> (0–20%); <i>Alnus</i> (0–15%); <i>Illex</i> (0–8%); <i>Podocarpus</i> (0–5%) and <i>Drymis</i> (0–2%)	Humaitá (HU01, 7° 55' 26" S/63° 04' 59" W) and Porto Velho (PV02, 8° 46' 43" S/63° 56' 48" W)		42,600–35,200	Cohen et al. (2014)

between the late Pleistocene and Holocene vegetation at the studied area. This new pollen record added to previously published multiple proxy data from the study area allowed to expand the geographical extension of late Pleistocene Andean trees, found today only at altitudes higher than 2000–3000 m. Future analysis of arboreal and herb pollen along the studied cores could contribute to improve the discussions of the LGM and Holocene climate. However, such analysis is complicated as herbaceous pollen grains from lake and floodplain sediments in the Humaitá region could be sourced from savannas formed by sedimentary processes, rather than climatic changes, which are also present over the Madeira River terraces.

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References

Abbott, M., Wolfe, B.B., Aravena, R., Wolfe, A.P., Seltzer, G.O., 2000. Holocene hydro-logical reconstructions from stable isotopes and paleolimnology, Cordillera Real, Bolivia. *Quat. Sci. Rev.* 19, 1801–1820.

Ab'Saber, A.N., 1977. Espaços ocupados pela expansão dos climas secos na América do Sul, por ocasião dos períodos glaciais quaternários. *Paléo* 1–19.

Absy, M.L., 1975. Polen e esporos do Quaternário de Santos (Brasil). *Hoehnea* 5, 1–26.

Absy, M.L., 1979. A Palynological Study of Holocene Sediments in the Amazon Basin. University of Amsterdam.

Absy, M., Clef, A., Fournier, M., 1991. Mise en évidence de quatre phases d'ouverture de la forêt dense dans le sud-est de l'Amazonie au cours des 60 000 dernières années. Première comparaison avec d. *Comptes rendus l'.*

Amaral, D.D., Mantelli, L.R., Rossetti, D. de F., 2012. Palaeoenvironmental control on modern forest composition of southwestern Marajó Island, Eastern Amazonia. *Water Environ. J.* 26, 70–84.

Anderson, J.B., Shipp, S.S., Lowe, A.L., Wellner, J.S., Mosola, A.B., 2002. The Antarctic Ice Sheet during the Last Glacial Maximum and its subsequent retreat history: a review. *Quat. Sci. Rev.* 21, 49–70.

Anhuf, D., Ledru, M.-P., Behling, H., Da Cruz, F.W., Cordeiro, R.C., Van der Hammen, T., Karmann, I., Marengo, J.A., De Oliveira, P.E., Pessenda, L., Sifeddine, A., Albuquerque, A.L., Da Silva Dias, P.L., 2006. Paleo-environmental change in Amazonian and African rainforest during the LGM. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 239, 510–527.

Argollo, J., Mourguiart, P., 2000. Late Quaternary climate history of the Bolivian Altiplano. *Quat. Int.* 72, 37–51.

Baker, P.A., Seltzer, G.O., Fritz, S.C., Dunbar, R.B., Grove, M.J., Tapia, P.M., Cross, S.L., Rowe, H.D., Broda, J.P., 2001. The history of South American tropical precipitation for the past 25,000 years. *Science* 291, 640–643.

Beerling, D.J., Mayle, F.E., 2006. Contrasting effects of climate and CO₂ on Amazonian ecosystems since the last glacial maximum. *Glob. Chang. Biol.* 12, 1977–1984.

Behling, H., 2001. Late Quaternary environmental changes in the Lagoa da Curuça region (eastern Amazonia, Brazil) and evidence of *Podocarpus* in the Amazon lowland. *Veg. Hist. Archaeobotany* 10, 175–183.

Behling, H., Cohen, M.L., Lara, R., 2004. Late Holocene mangrove dynamics of Marajó Island in Amazonia, northern Brazil. *Veg. Hist. Archaeobotany* 13, 73–80.

Bertani, T.C., Rossetti, D.F., Hayakawa, E.H., Cohen, M.C.L., 2015. Understanding Amazonian fluvial rias based on a Late Pleistocene-Holocene analog. *Earth Surf. Process. Landf.* 40, 285–292.

Burbridge, R.E., Mayle, F.E., Killeen, T.J., 2004. Fifty-thousand-year vegetation and climate history of Noel Kempff Mercado National Park, Bolivian Amazon. *Quat. Res.* 61, 215–230.

Bush, M.B., 1994. Amazonian speciation: a necessarily complex model. *J. Biogeogr.* 21, 5–17.

Bush, M.B., 2000. Deriving response matrices from central American modern pollen rain. *Quat. Res.* 54, 132–143.

Bush, M.B., 2002. Distributional change and conservation on the Andean flank: a palaeoecological perspective. *Glob. Ecol. Biogeogr.* 11, 463–473.

Bush, M.B., Colinvaux, P.A., Wiemann, M.C., Piperno, D.R., Liu, K., 1990. Late pleistocene temperature depression and vegetation change in Ecuadorian Amazonia. *Quat. Res.* 34, 330–345.

Bush, M., Piperno, D.R., Colinvaux, P.A., De Oliveira, P., Krissek, L., Miller, M., Rowe, W., 1992. A 14,300 year paleoecological profile of a lowland tropical lake in Panama. *Ecol. Monogr.* 62, 251–275.

Bush, M.B., Miller, M.C., De Oliveira, P.E., Colinvaux, P.A., 2002. Orbital forcing signal in sediments of two Amazonian lakes. *J. Paleolimnol.* 27, 341–352.

Bush, M.B., Silman, M.R., Urrego, D.H., 2004. 48,000 years of climate and forest change in a biodiversity hot spot. *Science* 303, 827–829.

Bush, M.B., Hansen, B.C.S., Rodbell, D.T., Seltzer, G.O., Young, K.R., Leon, B., Abbott, M.B., Silman, M.R., Gosling, W.D., 2005. A 17,000-year History of Andean Climatic and Vegetation Change From Laguna de Chochos, Peru.

Caputo, M.V., Rodriguez, R., Vasconcelos, D.N.N., 1972. Nomenclatura Estratigráfica da Bacia do Amazonas: histórico e atualização. In: SBG, Congr. Brasil. Geol., pp. 35–46 26°. Belém.

Cárdenas, M.L., Gosling, W.D., Sherlock, S.C., Poole, I., Pennington, R.T., Mothes, P., 2011. Response to comment on “The response of vegetation on the Andean flank in western Amazonia to Pleistocene climate change”. *Science* 333 (80-).

Cheng, H., Sinha, A., Cruz, F.W., Wang, X., Edwards, R.L., d'Horta, F.M., Ribas, C.C., Vuille, M., Stott, L.D., Auler, A.S., 2013. Climate change patterns in Amazonia and biodiversity. *Nat. Commun.* 4, 1411.

Clark, P.U., Seltzer, G.O., Hostetler, S.W., Clark, P.U., Goodman, A.Y., Rodbell, D.T., Seltzer, G.O., Mark, B.G., Benson, L.V., Dyke, A.S., McCabe, A.M., Clark, P.U., Vorren, T.O., Vorren, K.-D., Alm, T., Gulliksen, S., Lovlie, R., Blunier, T., Stuiver, M., Grootes, P.M., Wang, Y.J., Johnsen, S.J., Blunier, T., Brook, E.J., Alley, R.B., Brook, E.J., Anandakrishnan, S., Gosse, J.C., Klein, J., Evenson, E.B., Lawn, B., Middleton, R., Phillips, F.M., Thackrey, G.D., Hicock, S.R., Lian, O.B., Sturchio, N.C., Pierce, K.L., Murrell, M.T., Sorey, M.L., Grootes, P.M., Stuiver, M., White, J.W.C., Johnsen, S.J., Jouzel, J., Seltzer, G.O., Baker, P.A., Klein, A.G., Hostetler, S.W., Clark, P.U., Benson, L.V., Phillips, F.M., Mercer, J.H., Palacios, M.O., Clayton, J.D., Clapperton, C.M., Rodbell, D.T., Seltzer, G.O., Goodman, A.Y., Alley, R., Brook, E., Anandakrishnan, S., Broecker, W.S., Denton, G.H., 2002. Early deglaciation in the tropical Andes. *Science* 298, 7 (discussion 7).

Clark, P.U., Dyke, A.S., Shakun, J.D., Carlson, A.E., Clark, J., Wohlfarth, B., Mitrovica, J.X., Hostetler, S.W., McCabe, A.M., 2009. The Last Glacial Maximum. *Science* 325, 710–714.

CLIMAP, 1976. Climate: long-range investigation, mapping, and prediction (CLIMAP) project member. The surface of the ice-age earth, science. *Science* 191, 1131–1137 (80-).

Cohen, M.C.L., Rossetti, D.F., Pessenda, L.C.R., Friaes, Y.S., Oliveira, P.E., 2014. Late Pleistocene Glacial Forest of Humaitá-Western Amazonia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 415, 37–47.

Colinvaux, P.A., De Oliveira, P.E., 2001. Amazon plant diversity and climate through the Cenozoic. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 166, 51–63.

Colinvaux, P.A., De Oliveira, P.E., Moreno, J.E., Miller, M.C., Bush, M.B., 1996a. A long pollen record from lowland Amazonia: forest and cooling in glacial times. *Science* 274, 85–88 (80-).

Colinvaux, P.A., Liu, K.-B., de Oliveira, P., Bush, M.B., Iller, M.C., Annan, M.S., 1996b. Temperature depression in the lowland tropics in glacial times. *Clim. Chang.* 32,

- 19–33.
- Colinvaux, P.A., Bush, M.B., Steinitz-Kannan, M., Miller, M.C., 1997. Glacial and Postglacial Pollen Records from the Ecuadorian Andes and Amazon. *Quat. Res.* 48, 69–78.
- Colinvaux, P., De Oliveira, P.E., Patiño, J.E.M., 1999. *Amazon Pollen Manual and Atlas*. Harwood Academic Publishers, Dordrecht.
- Colinvaux, P.A., De Oliveira, P.E., Bush, M.B., 2000. Amazonian and neotropical plant communities on glacial time-scales: the failure of the aridity and refuge hypotheses. *Quat. Sci. Rev.* 19, 141–169.
- Constantine, J.A., Dunne, T., 2008. Meander cutoff and the controls on the production of oxbow lakes. *Geology* 36, 23.
- Cordeiro, R.C., Turcotte, B., Sifeddine, A., Lacerda, L.D., Silva Filho, E.V., Gueiros, B., Potty, Y.P., Santelli, R.E., Pádua, E.O., Patchinellam, S.R., 2011. Biogeochemical indicators of environmental changes from 50 Ka to 10 Ka in a humid region of the Brazilian Amazon. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 299, 426–436.
- Cunha, P.R.C., Gonzaga, F.G., Coutinho, L.F.C., Feijó, F.J., 1994. Bacia do Amazonas. *Bol. Geociências da Petrobras* 1, 47–55.
- D'Apolito, C., Absy, M.L., Latrubesse, E.M., 2013. The Hill of Six Lakes revisited: new data and re-evaluation of a key Pleistocene Amazon site. *Quat. Sci. Rev.* 76, 140–155.
- Davis, M.B., Deevey, E.S., 1964. Pollen accumulation rates: estimates from late-glacial sediment of Rogers Lake. *Science* 145, 1293–1295.
- Davis, M.B., Brubaker, L., Webb, L., 1973. Calibration of absolute pollen influx. In: Birks, H.J.B., West, R.G. (Eds.), *Quaternary Plant Ecology*. Blackwell Science, Oxford, pp. 9–25.
- Denton, G.H., Hughes, T.J., 2002. Reconstructing the Antarctic Ice Sheet at the Last Glacial Maximum. *Quat. Sci. Rev.* 21, 193–202.
- Eiras, J.F., Becker, C.R., Souza, E.M., Gonzaga, J.E.F., Silva, L.M., Daniel, L.M.F., Matsuda, N.S., Feijó, F.J., 1994. Bacia do Solimões. *Bol. Geociências da PETROBRAS* 8, 17–45.
- Faegri, K., 1971. The preservation of sporopollenin membranes under natural conditions. In: Brooks, J., Grant, P.R., Muir, M., Gijzel, P.V., Shaw, G. (Eds.), *Sporopollenin*. Academic Press, London, New York, pp. 256–270.
- Faegri, K., Iversen, J., 1989. *Textbook of Pollen Analyses*. John Wiley and Sons, New York.
- França, M.C., Cohen, M.C.L., Pessenda, L.C.R., Rossetti, D.F., Lorente, F.L., Buso Junior, A.A., Guimarães, J.T.F., Friaes, Y., Macario, K., 2013. Mangrove vegetation changes on Holocene terraces of the Doce River, southeastern Brazil. *Catena* 110, 59–69.
- Furlow, J., Furlow, J., 1979. The systematics of the American species of *Alnus* (Betulaceae) [concl.]. *Rhodora* 81, 151–248.
- Ganopolski, A., Rahmstorf, S., Petoukhov, V., Claussen, M., 1998. Simulation of modern and glacial climates with a coupled global model of intermediate complexity. *Nature* 391, 351–356.
- Gasse, F., Van Campo, E., 1998. A 40,000-yr pollen and diatom record from Lake Tritrivakely, Madagascar, in the southern tropics. *Quat. Res.* 49, 299–311.
- Gosling, W.D., Mayle, F.E., Tate, N.J., Killeen, T.J., 2009. Differentiation between Neotropical rainforest, dry forest, and savannah ecosystems by their modern pollen spectra and implications for the fossil pollen record. *Rev. Palaeobot. Palynol.* 153, 70–85.
- Grimm, E.C., 1987. CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Comput. Geosci.* 13, 13–35.
- Grindrod, J., 1988. The palynology of holocene mangrove and saltmarsh sediments, particularly in Northern Australia. *Rev. Palaeobot. Palynol.* 55, 229–245.
- Guilderson, T.P., Fairbanks, R.G., Rubenstone, J.L., 1994. Tropical temperature variations since 20,000 years ago: modulating interhemispheric climate change. *Science* 263, 663–665.
- Haberle, S., 1997. Upper Quaternary vegetation and climate history of the Amazon basin: correlating marine and terrestrial pollen records. In: Flood, R.D., Piper, D.J.W., Klaus, A., Peterson, L.C. (Eds.), *Proceedings of the Ocean Drilling Program, Scientific Results*. College Station, pp. 381–396.
- Haffer, J., 1969. Speciation in amazonian forest birds. *Science* 165 (3889), 131–137.
- Haffer, J., Prance, G.T., 2001. Climatic forcing of evolution in Amazonia during the Cenozoic: on the refuge theory of biotic differentiation. *Amazoniana* 16, 579–607.
- Hager, W.H., Hutter, K., 1984. Approximate treatment of plane channel flow. *Acta Mech.* 51, 31–48.
- van der Hammen, T., Absy, M.L., 1994. Amazonia during the last glacial. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 109, 247–261.
- Harper, C.W.J., 1984. Improved Methods of Facies Sequence Analysis, Facies Models: Response to Sea Level Change. In: *Geological Association of Canada, Reprint Series*. 1, pp. 11–13.
- Havinga, A.J., 1967. Palynology and pollen preservation. *Rev. Paleobotany Palynol.* 2, 81–98.
- Hayakawa, E.H., Rossetti, D.F., Valeriano, M.M., 2010. Applying DEM-SRTM for reconstructing a Late Quaternary paleodrainage in Amazonia. *Earth Planet. Sci. Lett.* 297, 262–270.
- Huybrechts, P., 2002. Sea-level changes at the LGM from ice-dynamic reconstructions of the Greenland and Antarctic ice sheets during the glacial cycles. *Quat. Sci. Rev.* 21, 203–231.
- Irion, G., 1982. Mineralogical and geochemical contribution to climatic history in central Amazonia during Quaternary time. *Trop. Ecol.* 23, 76–85.
- Jeong, G.Y., Cheong, C.-S., Choi, J.-H., 2007. The effect of weathering on optically stimulated luminescence dating. *Quat. Geochronol.* 2, 117–122.
- Keshavarzi, A., Habibi, L., 2005. Optimizing water intake angle by flow separation analysis. *Irrig. Drain.* 54, 543–552.
- Klein, A.G., Seltzer, G.O., Isacks, B.L., 1999. Modern and last local glacial maximum snowlines in the Central Andes of Peru, Bolivia, and Northern Chile. *Quat. Sci. Rev.* 18, 63–84.
- Latrubesse, E.M., Franzinelli, E., 2002. The Holocene alluvial plain of the middle Amazon River, Brazil. *Geomorphology* 44, 241–257.
- Law, S.W., Reynolds, A.J., 1966. Dividing flow in an open channel. *J. Hydraul. Div. Am. Soc. Civ. Eng.* 92, 207–231.
- Ledru, M.-P., 1993. Late Quaternary environmental and climatic changes in Central Brazil. *Quat. Res.* 39, 90–98.
- Ledru, M.-P., Cordeiro, R.C., Dominguez, J.M.L., Martin, L., Mourguiart, P., Sifeddine, A., Turcotte, B., 2001. Late-glacial cooling in Amazonia inferred from pollen at Lagoa do Caçó, Northern Brazil. *Quat. Res.* 55, 47–56.
- Leroux, M., 1993. The Mobile Polar High: a new concept explaining present mechanisms of meridional air-mass and energy exchanges and global propagation of palaeoclimatic changes. *Glob. Planet. Chang.* 7, 69–93.
- Liu, K., Colinvaux, P.A., 1985. Forest changes in the Amazon Basin during the last glacial maximum. *Nature* 318, 556–557.
- Macedo, R.B., 2009. Análise palinológica de um testemunho holocênico em Santo Antônio da Patrulha, Rio Grande do Sul. *Federal University of Rio Grande do Sul, Brasil*.
- Markgraf, V., D'Antoni, H.L., 1978. *Pollen Flora of Argentina*. University of Arizona Press, Tucson.
- Maslin, M.A., Ettwein, V.J., Wilson, K.E., Guilderson, T.P., Burns, S.J., Leng, M.J., 2011. Dynamic boundary-monsoon intensity hypothesis: evidence from the deglacial Amazon River discharge record. *Quat. Sci. Rev.* 30, 3823–3833.
- Maslin, M.A., Ettwein, V.J., Boot, C.S., Bendle, J., Pancost, R.D., 2012. Amazon Fan biomarker evidence against the Pleistocene rainforest refuge hypothesis? *J. Quat. Sci.* 27, 451–460.
- Mayle, F.E., Beerling, D.J., 2004. Late Quaternary changes in Amazonian ecosystems and their implications for global carbon cycling. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 214, 11–25.
- Mayle, F.E., Burbridge, R., Killeen, T.J., 2000. Millennial-scale dynamics of southern Amazonian rain forests. *Science* 290, 2291–2294.
- Mayle, F.E., Burn, M.J., Power, M., Urrego, D.H., 2009. *Vegetation and Fire at the Last Glacial Maximum in Tropical South America*. Springer, Netherlands, pp. 89–112.
- Mischke, S., Lai, Z., Aichner, B., Heinecke, L., Mahmoudov, Z., Kuessner, M., Herzscheuh, U., 2017. Radiocarbon and optically stimulated luminescence dating of sediments from Lake Karakul, Tajikistan. *Quat. Geochronol.* 41, 51–61.
- Mook, W.G., van de Plassche, O., 1986. Radiocarbon dating. In: van de Plassche, O. (Ed.), *Sea-Level Research: A Manual for the Collection and Evaluation of Data*. Geo Books, Norwich, pp. 525–560.
- Mosblech, N.A.S., Bush, M.B., Gosling, W.D., Hodell, D., Thomas, L., van Calsteren, P., Correa-Metrio, A., Valencia, B.G., Curtis, J., van Woesik, R., 2012. North Atlantic forcing of Amazonian precipitation during the last ice age. *Nat. Geosci.* 5, 817–820.
- Mourguiart, P., Corrége, T., Wirmann, D., Argollo, J., Montenegro, M., Pourchet, M., Carbonel, P., 1998. Holocene palaeohydrology of Lake Titicaca estimated from an ostracod-based transfer function. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 143, 51–72.
- Murray, A.S., Olley, J.M., 2002. Precision and accuracy in the optically stimulated luminescence dating of sedimentary quartz: a status review. *Geochronometria J. Methods Appl. Absol. Chronol.* 21, 1–16.
- Nakada, M., Kimura, R., Okuno, J., Moriwaki, K., Miura, H., Maemoku, H., 2000. Late Pleistocene and Holocene melting history of the Antarctic ice sheet derived from sea-level variations. *Mar. Geol.* 167, 85–103.
- Nierop, K.G., Buurman, P., de Leeuw, J.W., 1999. Effect of vegetation on chemical composition of H horizons in incipient podzols as characterized by ¹³C NMR and pyrolysis-GC/MS. *Geoderma* 90, 111–129.
- Orlova, L.A., Panychev, V.A., 1993. The reliability of radiocarbon dating buried soils. *Radiocarbon* 35, 369–377.
- Paduano, G.M., Bush, M.B., Baker, P.A., Fritz, S.C., Seltzer, G.O., 2003. A vegetation and fire history of Lake Titicaca since the Last Glacial Maximum. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 194, 259–279.
- Pessenda, L.C.R., Valencia, E.P.E., Martinelli, L.A., Cerri, C.C., 1996. ¹⁴C measurements in tropical soil developed on basic rocks. *Radiocarbon* 38 (2), 203–208.
- Pessenda, L.R., Gouveia, S.M., Aravena, R., 2001. Radiocarbon dating of total soil organic matter and humin fraction and its comparison with (super 14) C ages of fossil charcoal. *Radiocarbon* 43, 595–601.
- Pessenda, L.C.R., De Oliveira, P.E., Mofatto, M., de Medeiros, V.B., Francischetti Garcia, R.J., Aravena, R., Bendassoli, J.A., Zuniga Leite, A., Saad, A.R., Lincoln Etchebehere, M., 2009. The evolution of a tropical rainforest/grassland mosaic in southeastern Brazil since 28,000 ¹⁴C yr BP based on carbon isotopes and pollen records. *Quat. Res.* 71, 437–452.
- Piperno, D.R., Bush, M.B., Colinvaux, P.A., 1990. Paleoenvironments and human occupation in late-glacial Panama. *Quat. Res.* 33, 108–116.
- Pollard, D., DeConto, R.M., 2009. Modelling West Antarctic ice sheet growth and collapse through the past five million years. *Nature* 458, 329–332.
- Preusser, F., Degering, D., Fuchs, M., Hilgers, A., Kaderit, A., Klasen, N., Krbetschek, M., Richter, D., Spencer, J.Q.G., 2008. Luminescence dating: basics, methods and applications. *Eiszeitalter und Gegenwart Quat. Sci. J.* 57, 1–2.
- Punyasaena, S.W., Dalling, J.W., Jaramillo, C., Turner, B.L., 2011. Comment on “The response of vegetation on the Andean flank in western Amazonia to Pleistocene climate change”. *Science* 333, 1825 (author reply 1825).
- Räsänen, M., Salo, J., Kalliola, R., 1987. Fluvial perturbation in the western Amazon basin: regulation by long term sub-Andean tectonics. *Science* 238, 1398–1401 (80-).
- Reese, C.A., Liu, K.-B., 2005. A modern pollen rain study from the central Andes region of South America. *J. Biogeogr.* 32, 709–718.
- Reimer, P., 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon* 55, 1869–1887.
- Rind, D., 2000. Relating paleoclimate data and past temperature gradients: some

- suggestive rules. *Quat. Sci. Rev.* 19, 381–390.
- Rossetti, D.F., Góes, A.M., Valeriano, M.M., Miranda, M.C.C., 2008. Quaternary tectonics in a passive margin: Marajó Island, northern Brazil. *J. Quat. Sci.* 23, 121–135.
- Rossetti, D.F., Cohen, M.C.L., Tatum, S.H., Sawakuchi, A.O., Cremon, É.H., Mittani, J.C.R., Bertani, T.C., Munita, C.J.A.S., Tudela, D.R.G., Yee, M., Moya, G., 2015. Mid-Late Pleistocene OSL chronology in western Amazonia and implications for the transcontinental Amazon pathway. *Sediment. Geol.* 330, 1–15.
- Rossetti, D.F., Cohen, M.C.L., Pessenda, L.C.R., 2017. Vegetation change in southwestern Amazonia (Brazil) and relationship to the late pleistocene and holocene climate. *Radiocarbon* 59.
- Roubik, D.W., Moreno, J.E., 1991. Pollen and Spores of Barro Colorado Island. Missouri Botanical Garden.
- Rull, V., 2013. Palaeoclimates and Amazon biodiversity. *J. Biogeogr.* 40, 1413–1414.
- Salgado-Labouriau, M.L., 1973. Contribuição à palinologia dos cerrados. Academia Brasileira de Ciências, Rio de Janeiro.
- Sant'Anna, L.G., Soares, E.A. do A., Riccomini, C., Tatum, S.H., Yee, M., 2017. Age of depositional and weathering events in Central Amazonia. *Quat. Sci. Rev.* 170, 82–97.
- Sawakuchi, A.O., Kalchgruber, R., Giannini, P.C.F., Nascimento Jr., D.R., Guedes, C.C.F., Umisedo, N.K., 2008. The development of blowouts and foredunes in the Ilha Comprida barrier (Southeastern Brazil): the influence of Late Holocene climate changes on coastal sedimentation. *Quat. Sci. Rev.* 27, 2076–2090.
- Sifeddine, A., Fröhlich, F., Fournier, M., Martin, L., Servant, M., Soubiès, F., Turco, B., Suguio, K., Volkmer-Ribeiro, C., 1994. La sédimentation lacustre indicateur de changements des paléoenvironnements au cours des 30000 dernières années (Carajas, Amazonie, Brésil). *Compte Rendus l'Académie des Sci.* 318, 1645–1652.
- Sifeddine, A., Martin, L., Turcq, B., Volkmer-Ribeiro, C., Soubiès, F., Cordeiro, R.C., Suguio, K., 2001. Variations of the Amazonian rainforest environment: a sedimentological record covering 30,000 years. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 168, 221–235.
- Smith, J.A., Seltzer, G.O., Farber, D.L., Rodbell, D.T., Finkel, R.C., 2005. Early local last glacial maximum in the tropical Andes. *Science* 308, 678–681.
- Stevenson, F.J., 1994. Humus Chemistry. Genesis, Composition, Reactions, 2a ed. John Wiley, New York.
- Stute, M., Talma, A.S., 1998. Glacial Temperatures and Moisture Transport Regimes Reconstructed From Noble Gases and $\delta^{18}\text{O}$. Stampriet aquifer, Namibia.
- Stute, M., Forster, M., Frischkorn, H., Serejo, A., Clark, J.F., Schlosser, P., Broecker, W.S., Bonani, G., 1995. Cooling of tropical Brazil (5°C) during the last glacial maximum. *Science* 269, 379–383.
- Thompson, L.G., Mosley-Thompson, E., Davis, M.E., Lin, P.N., Henderson, K.A., Cole-Dai, J., Bolzan, J.F., Liu, K.B., 1995. Late glacial stage and holocene tropical ice core records from Huascarán, Peru. *Science* 269, 46–50 (80-).
- Tricart, J., 1985. Evidence of Upper Pleistocene dry climates in northern South America. 197–217.
- Urrego, D.H., Silman, M.R., Bush, M.B., 2005. The Last Glacial Maximum: stability and change in a western Amazonian cloud forest. *J. Quat. Sci.* 20, 693–701.
- Van der Hammen, T., 2000. Aspectos de historia y ecología de la biodiversidad norandina y amazónica. *Rev. la Acad. Colomb. Ciencias Exactas, Físicas y Nat.* 24, 231–245.
- Van Der Hammen, T., Hooghiemstra, H., 2000. Neogene and Quaternary History of Vegetation, Climate, and Plant Diversity in Amazonia. pp. 19.
- Van Meerbeek, C.J., Renssen, H., Roche, D.M., 2009. How did Marine Isotope Stage 3 and last glacial maximum climates differ? – perspectives from equilibrium simulations. *Clim. Past* 5, 33–51.
- Vanzolini, P.E., Williams, E.E., 1981. The vanishing refuge: a mechanism for ecogeographic speciation. *Pap. Avulsos Zool.* 34, 251–255.
- Vidotto, E., Carlos, L., Pessenda, R., Ribeiro, A.D.S., De, H.A., Bendassolli, J.A., 2007. Dinâmica do ecótono floresta-campo no sul do estado do Amazonas no Holoceno, através de estudos isotópicos e fitossociológicos. 37, 385–400.
- Walker, R.G., 1992. Facies, facies models and modern stratigraphic concepts. In: Walker, R.G., James, N.P. (Eds.), *Facies Models - Response to Sea Level Change*. Geological Association of Canada, Ontario, pp. 1–14.
- Wang, X., Edwards, R.L., Auler, A.S., Cheng, H., Kong, X., Wang, Y., Cruz, F.W., Dorale, J.A., Chiang, H.-W., 2017. Hydroclimate changes across the Amazon lowlands over the past 45,000 years. *Nature* 541, 204–207.
- Webb, R.S., Rind, D.H., Lehman, S.J., Healy, R.J., Sigman, D., 1997. Influence of ocean heat transport on the climate of the Last Glacial Maximum. *Nature* 385, 695–699.
- Weber, M.E., Clark, P.U., Ricken, W., Mitrovica, J.X., Hostetler, S.W., Kuhn, G., 2011. Interhemispheric ice-sheet synchronicity during the Last Glacial Maximum. *Science* 334, 1265–1269.
- Weng, C., Bush, M.B., Chepstow-Lusty, A.J., 2004a. Holocene changes of Andean alder (*Alnus acuminata*) in highland Ecuador and Peru. *J. Quat. Sci.* 19, 685–691.
- Weng, C., Bush, M.B., Silman, M.R., 2004b. An analysis of modern pollen rain on an elevational gradient in southern Peru. *J. Trop. Ecol.* 20, 113–124.
- Weng, C., Hooghiemstra, H., Duivenvoorden, J.F., 2006. Challenges in estimating past plant diversity from fossil pollen data: statistical assessment, problems, and possible solutions. *Divers. Distrib.* 12, 310–318.
- Ybert, J.P., 1992. Ancient lake environments as deduced from pollen analysis. In: DeJoux, C., Iltis, A. (Eds.), *Lake Titicaca: A Synthesis of Limnological Knowledge*. Kluwer Academic Publishers, Boston, pp. 49–62.